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RESEARCH ARTICLE

A Quantitative Classification of the Geography of Non-Native Flora in the United States

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ABSTRACT

Aim: Non-native plants have the potential to harm ecosystems. Harm is classically related to their distribution and abundance, but this geographical information is often unknown. Here, we assess geographical commonness as a potential indicator of invasive status for non-native flora in the United States. Geographical commonness could inform invasion risk assessments across species and ecoregions.

Location: Conterminous United States.

Time Period: Through 2022.

Major Taxa Studied: Plants.

Methods: We compiled and standardised occurrence and abundance data from 14 spatial datasets and used this information to categorise non-native species as uncommon or common based on three dimensions of commonness: area of occupancy, habitat breadth and local abundance. To assess consistency in existing categorizations, we compared commonness to invasive status in the United States. We identified species with higher-than-expected abundance relative to their occupancy, habitat breadth or

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residence time. We calculated non-native plant richness within United States ecoregions and estimated unreported species based on rarefaction/extrapolation curves.

Results: This comprehensive database identified 1874 non-native plant species recorded in 4,844,963 locations. Of these, 1221 species were locally abundant (> 10% cover) in 797,759 unique locations. One thousand one hundred one non-native species (59%) achieved at least one dimension of commonness, including 565 species that achieved all three. Species with longer residence times tended to meet more dimensions of commonness. We identified 132 species with higher-than-expected abundance. Ecoregions in the central United States have the largest estimated numbers of unreported, abundant non-native plants.

Main Conclusions: A high proportion of non-native species have become common in the United States. However, existing categorizations of invasive species are not always consistent with species' abundance and distribution, even after considering residence time. Considering geographical commonness and higher-than-expected abundance revealed in this new dataset could support more consistent and proactive identification of invasive plants and lead to more efficient management practices.

1 | Introduction

Whether a species is rare or common influences its interaction with other species as well as its effects on ecosystem structure and function (Gaston 2011). For non-native species, commonness is a concern because it might be linked to the potential to invade (i.e., invasiveness *sensu* Catford et al. 2016), which by definition leads to ecological harm (Roy et al. 2023). Metrics of commonness have been proposed for and applied to non-native plants in order to characterise their range dynamics and infer potential risk (McGeoch and Latombe 2016; Fristoe et al. 2021). However, for most regions, comprehensive analyses of the biogeography of non-native species are lacking. Frameworks for quantitatively determining commonness are incomplete and, as a consequence, managers and policymakers may fail to identify potentially invasive species in time to prevent ecological harm.

Our understanding of invasive species is often based on expert knowledge (e.g., Randall 2017; Simpson et al. 2022) and does not integrate empirical measures of commonness, leading to a high level of uncertainty in the identification of invasive species (McGeoch et al. 2012). For invasive plants in the United States, this leads to inconsistent management and regulation because definitions of what is invasive depend on available expertise and capacity, which vary across political borders (Lakoba et al. 2020; Beaury et al. 2021). Invasion science further suffers from a scientific literature that is biased towards a small proportion of taxa (Pyšek et al. 2008) and has likely failed to identify over 1/3 of currently invasive plants (Laginhas et al. 2023). Focusing on the macroecological patterns of non-native plant commonness might help to inform assessments of invasion risk at the regional to sub-regional scales most appropriate for invasive species management.

Dimensions of species rarity were first presented by Rabinowitz (1981) in terms of range size (small vs. large), habitat specificity (narrow vs. wide) and local population size (sparse vs. locally abundant). Although described in terms of rarity (Rabinowitz 1981), these same dimensions can also be used to define species commonness (e.g., Godet et al. 2015), and have been proposed and used for the analysis of potentially invasive species (Catford et al. 2016; McGeoch and Latombe 2016; Fristoe et al. 2021). Non-native species tend to be more common than native species (Hansen et al. 2013), and common species often have an outsized impact on native community assemblages (e.g., Lennon et al. 2004) and ecosystem function (Gaston 2011). Similarly, non-native species impact native species and recipient communities in proportion to their abundance, meaning that common non-natives have the greatest impact (e.g., Bradley et al. 2019). Indeed, the ecological impact of non-native species has been classically thought to relate to dimensions of commonness (including species range size and local abundance; Parker et al. 1999). Thus, common non-native species are expected to cause greater ecological harm, leading to their categorisation as invasive (Catford et al. 2016; Gaston et al. 2000).

The dimensions of commonness are predicted to covary (Gaston 2003). Species with large areas of occupancy are likely to exist in multiple habitats. Similarly, abundant populations are expected to lead to range expansion and a larger area of occupancy (Gaston 2003). However, relationships between dimensions of commonness have only been described in a few cases, and the processes underlying occurrence can differ from those underlying local abundance, leading to weak relationships (Sporbert et al. 2020). Fristoe et al. (2021) analysed non-native plants in Europe and found a moderate correlation between local abundance and range size ($r = 0.48$) and a weaker correlation between range size and habitat breadth ($r = 0.23$). Using a similar approach to assess correlations between dimensions of commonness for non-native plants in other regions can help to inform the generality of the macroecological patterns of commonness. Additionally, deviations from expected relationships could help to identify non-native species that might pose higher or lower risk of invasion. Species with higher-than-expected abundance relative to their range size may have larger local impacts (Sofaer et al. 2018; Bradley et al. 2019; Pearse et al. 2019) and be a higher risk to ecosystems. In contrast, species with lower-than-expected abundance relative to their range size might be less likely to cause ecological harm, such as species that become abundant following disturbance (MacDougall and Turkington 2005). Thus, species with higher-than-expected abundance relative to their distribution may be more likely to be invasive.

Another important factor influencing the dimensions of commonness for non-native species is time since establishment, or residence time. Residence time is often correlated with range size (Pyšek and Jarošík 2006; Gassó et al. 2009), as newly established species may not have had an opportunity to spread. Widespread human-mediated introductions could shorten the time it takes for non-native species to fill their potential ranges (Bradley et al. 2024), but it could take more than 150 years for some species to reach their maximum distribution range (Gassó et al. 2010). As a result, McGeoch and Latombe (2016) advocate for including residence time as a covariate when measuring dimensions of commonness. As expected, Fristoe et al. (2021) found that residence time was significantly related to abundance, range size and habitat breadth in non-native European plants. Species with a larger-than-expected number of abundant populations despite a short residence time may be more likely to be invasive.

Considering dimensions of commonness as indicators of biological invasions can potentially uncover species in the early stages of invasion and lead to more targeted invasive species risk assessments for specific regions. Lists of invasive plants already exist globally and for many nations (e.g., Laginhas and Bradley 2022), and within the United States, the Register of Introduced and Invasive Species (RIIS) distinguishes between non-native species that are established versus non-native species that are invasive based on expert knowledge and assessments of state and federal scientists and practitioners (Simpson et al. 2022). However, the broad geographic scale of global and national lists poses a challenge for local and landscape scale management because plant species categorised as invasive are rarely invasive everywhere in their non-native range (Bradley 2013; Ibáñez et al. 2023). Although both international and national lists reflect the expert knowledge of smaller jurisdictions, local assessments often suffer from a lack of resources, leading to spatial and taxonomic biases (Pyšek et al. 2008; Laginhas et al. 2023) and an over-emphasis on well-known invasives in management and regulation in the United States (Buerger et al. 2016; Beaury et al. 2021; Bradley et al. 2022). Thus, compiling geographical information about all non-native species can help to identify the lesser-known species that are likely to establish and become abundant at local scales, leading to more actionable watchlists of potentially invasive plants at the scale of feasible management (e.g., Jarnevich et al. 2023). Moreover, geographical information can also be used to estimate total numbers of non-native species (i.e., non-native species richness) and thus to identify hot spots of invasion (Ibáñez et al. 2009) to inform the magnitude of need for non-native species monitoring and management.

Here, we demonstrate the use of a commonness framework for understanding geographic patterns of invasive species abundance and richness. We first compiled a comprehensive database of non-native plant distribution and abundance across the conterminous United States (CONUS) and identified species achieving one or more of the three dimensions of commonness. We use this database to address the following three questions: (1) How are quantitatively based dimensions of commonness related to expert-identified invasiveness?; (2) Can correlations between range size, habitat specificity, local abundance, and residence time help to identify potentially high-risk invasive species? and (3) Which geographic regions are failing to identify or record large portions of their non-native plant species pool?

2 | Materials and Methods

2.1 | Database Compilation

In 2021–2022, we acquired spatially explicit data from 14 repositories that included information about non-native/invasive plants or full plant communities (Table 1). The non-native/invasive plant repositories (e.g., iMap Invasives, EDDMapS) focused on species identified as potentially problematic by natural resource managers and contained both weedy native plants and invasive non-native plants. Plants native to all or part of the CONUS represented $<2\%$ of all occurrence data and $<1\%$ of all abundance data and were excluded from the analysis. The datasets representing full plant communities were taken largely from the Standardised Plant Community with Introduced Status database (SPCIS; Petri et al. 2023), although we retained the original dataset names (Table 1). For plant community datasets, we retained only species identified as non-native ('introduced') to the lower 48 states or to North America by the USDA Plants database (USDA PLANTS 2023). We excluded the Forest Inventory and Analysis (FIA) community data in SPCIS because precise plot locations were obscured, making the dataset unsuitable for this analysis. Some datasets included subspecies and varieties, which we recategorised to the species level. We retained 11 species hybrids. For all included datasets, we standardised species names to the USDA Plants taxonomy and appended the accepted species code (USDA PLANTS 2023). We retained year sampled, unique plot identifiers, latitude, and longitude from the source datasets (Table 1). We excluded points located outside of the CONUS and removed duplicate records.

2.1.1 | Categorising High Abundance

Although the majority of data were occurrence only, many observations also included information about non-native plant abundance. Abundance information in the datasets included percent cover (0%–100%), cover class (e.g., 1%–5%, 6%–10%), stem count ranges (e.g., 1–10, 11–100), and qualitative measures of abundance (e.g., trace, moderate, dense). We transformed cover class and stem count ranges into single values using the average of range minimum and maximum (e.g., 1%–5% was transformed to 3%). We categorised point locations as containing abundant infestations if they reported non-native species percent cover $>10\%$, average cover class $>10\%$, average stem count >1000, or qualitative abundance values of 'high', 'dense', 'monoculture', 'abundant' or 'common.' Percent cover and cover class thresholds were chosen based on past analyses that differentiated between occurrence and abundance (Jarnevich et al. 2021; Beaury, Jarnevich, et al. 2023). The stem count threshold was arbitrary, but stem count metrics were reported in only one dataset and represent $<0.01\%$ of the dataset (Table 1). Measurement area is rarely reported in invasive plant repositories (Bradley et al. 2018), thus abundance metrics could apply to any observed area from a small patch to several hectares. We used all occurrence data to evaluate habitat breadth and area of occupancy and the subset of locations reporting an abundant infestations to evaluate local abundance.

TABLE 1 | Counts of unique locations and species associated with abundant and total datasets compiled in this analysis.

Dataset	Access date	Pct Cov	Cov class	Stem count	Qual abund	*N* pts	*N* spp	Year range	Source
Invasive plant datasets (counts include only non-native species)									
CalFlora									
Abundant	6/2021	16,280	96,516	—	160	112,814	545	1899–2021	www.calflora.org
Total		39,019	159,423	—	602	198,844	670	1899–2021	
EDDMapS									
Abundant	6/2022	419,036	49,337	—	18,061	486,434	748	1899–2022	https://www.eddmaps.org/
Total		590,766	93,946	—	42,548	3,198,963	1501	1810–2022	
FLINV[a]									
Abundant	1/2021	—	38,766	—	—	38,766	106	2008–2010	—
Total		—	64,055	—	—	167,469	114	2008–2010	
iMap									
Abundant	6/2022	25,158	54,458	—	49,157	87,410	398	1900–2022	https://www.imapinvasives.org/
Total		33,638	91,787	—	162,040	910,675	871	1818–2022	
MISIN									
Abundant	6/2021	—	—	—	31,948	31,948	176	1981–2021	https://www.misin.msu.edu/
Total		—	—	—	168,320	189,975	271	1899–2021	
TXINV									
Abundant	5/2021	—	—	—	14,117	14,117	112	2005–2021	www.texasinvasives.org
Total		—	—	—	20,991	21,427	127	2005–2021	
Plant community datasets (counts include only non-native species)									
AIM									
Abundant	12/2022	11,873	—	—	—	11,873	122	2004–2019	Petri et al. (2023)
Total		35,231	—	—	—	35,231	311	2004–2019	
CVS									
Abundant	12/2022	434	—	—	—	434	41	1977–2015	Petri et al. (2023)
Total		6818	—	—	—	6818	274	1976–2015	

(Continues)

TABLE 1 | (Continued)

Dataset	Access date	Pct Cov	Cov class	Stem count	Qual abund	*N* pts	*N* spp	Year range	Source
GLIFWC									
Abundant	6/2021	—	—	1615	—	1615	94	1998–2020	https://glifwc.org/
Total		—	—	8140	—	8781	177	1994–2021	
IL CTAP									
Abundant	12/2020	1195	—	—	—	1195	69	1997–2019	https://publish.illinois.edu/ctap-inhs/
Total		6803	—	—	—	6804	179	1997–2019	
NEON									
Abundant	12/2022	144	—	—	—	144	37	2015–2019	NEON (2023a, 2023b), Petri et al. (2023)
Total		2656	—	—	—	2656	234	2015–2019	
NPS									
Abundant	12/2022	2700	—	—	—	2700	238	1991–2020	Petri et al. (2023)
Total		23,558	—	—	—	23,558	548	1990–2020	
NWCA									
Abundant	12/2022	1903	—	—	—	1903	200	2011–2016	Petri et al. (2023)
Total		12,499	—	—	—	12,499	490	2011–2016	
VegBank									
Abundant	5/2021	6406	—	—	—	6406	301	1972–2015	www.vegbank.org
Total		60,160	—	—	—	61,262	715	1972–2015	
All data									
Abundant		485,129	239,077	1615	113,443	797,759	1221		
Total		811,149	409,211	8140	394,501	4,844,963	1874		

Note: Numbers refer to the number of records reporting percent cover (Pct Cov), cover class (Cov Class), stem count, or qualitative abundance information (Qual Abund) broken down by records of abundant infestations and total occurrences. *N* pts. is the total number of records of abundant or present non-native species. *N* spp. is the richness of abundant or present non-native species. Year Range is the inclusive dates in the dataset. Source is the publication or website where data can be found (where applicable).

[a]Florida invasive species database.

2.1.2 | Categorising Species Commonness

Following previous approaches to analyse commonness (Rabinowitz 1981; Catford et al. 2016; McGeoch and Latombe 2016; Fristoe et al. 2021), we evaluated three dimensions of commonness that could be indicative of invasion risk: area of occupancy, habitat breadth, and local abundance. We measured the area of occupancy of individual species (i.e., identifying species that are widespread) as the number of 50-km maximal diameter hexagons spanning the CONUS that contained at least one of the species' occurrences. We focused on counts of hexagons rather than on counts of occurrences to ensure that we were measuring a proxy for range size rather than sampling effort (some species are heavily sampled within local geographies). We measured habitat breadth of individual species (i.e., identifying species that are generalists) as the number of unique Environmental Protection Agency (EPA) Level 3 ecoregions (Omernik and Griffith 2014) that contained at least one of the species' occurrences. Finally, we measured the abundance of individual species (i.e., identifying species that achieve local abundance) as a count of all records of abundant infestations (e.g., $>10\%$ cover; refer to description above). We counted all records of abundant infestations rather than the area of occupancy of abundant infestations under the assumption that a high number of reports are indicative of a larger infestation and a potentially more problematic species, even if the records were in close proximity.

Species that are more common might be more likely to cause ecological harm (Catford et al. 2016). To categorise non-native species as 'common', we compared the three dimensions of commonness to information from an independent dataset of non-native species status: the United States Register of Introduced and Invasive Species (RIIS; Simpson et al. 2022). RIIS identifies non-native species as established, invasive or widespread invasive based on the expert knowledge of natural resource managers as well as agency assessments aggregated from across the United States (Simpson et al. 2022). Because RIIS aggregates from multiple sources, many of which are not based on geography or quantitative assessment, we use RIIS to inform our categorization of commonness, but we do not assume that RIIS has correctly differentiated between invasive versus established species.

For each of the three dimensions of commonness, we defined 'common' using a threshold that excluded 75% of species categorised by RIIS as established (Appendix S1, Figure S1), assuming that the majority of established (but not invasive) species should be categorised as uncommon. This threshold is arbitrary but aims to err on the side of including more potentially problematic species as 'common' at the risk of also identifying some benign, established species as 'common'. This threshold also maximises overall classification accuracy when compared to the RIIS dataset such that established species are more likely to be categorised as uncommon whereas invasive species are more likely to be categorised as common (Appendix S1, Figure S1). To be classified as widespread, species had to be present in 12 or more of 5117 hexagons; to be classified as generalist, species had to be present in 5 or more of 86 EPA Level III ecoregions (Omernik and Griffith 2014); and to be classified as abundant, species had to have five or more records of abundant infestations. All other species were classified as uncommon. Species that met two or three dimensions of commonness were classified accordingly (e.g., 'abundant & widespread').

2.2 | Commonness Versus Invasiveness

To assess how commonness was associated with whether a species was categorised as invasive, we calculated the proportion of species in each commonness category that were identified as invasive by either the RIIS dataset (Simpson et al. 2022) or the Global Plant Invaders dataset (Laginhas and Bradley 2022). We fit a generalised linear model assuming a binomial distribution to test if the number of commonness categories a species met (0, 1, 2 or 3) predicted whether it was categorised as invasive by one of the two datasets. In other words, we asked how expert-informed classifications of invasion relate to the quantitative metrics of commonness described here.

2.3 | Correlations Between the Dimensions of Commonness

We assessed how dimensions of commonness are correlated with each other (Fristoe et al. 2021), and how each dimension is influenced by species' residence time in the United States. We appended information on minimum residence time using data from Williams et al. (2024), which documents the date and location of initial georeferenced observations of non-native taxa in the continental United States. Williams et al. (2024) uses the Integrated Taxonomic Information System (https://itis.gov) for scientific names, and we used the taxize package in R (Chamberlain and Szöcs 2013) to check our names for synonyms prior to joining. To calculate residence time, we took the difference between the year 2022 (the most recent records in our dataset) and the year of the first record of observation. Residence time was not available for 104 of the 1874 non-native species for which we compiled geographic data; these species were excluded from the correlation analysis involving residence time but were included in all other analyses.

To characterise associations between dimensions of commonness, we first took the $\log_{10}$ of hexagon count, ecoregion count, and count of abundant infestations (plus 1, to enable inclusion of species without records of abundance) to account for skewed data distributions. We estimated the Pearson correlation coefficient between each pair of variables. We also fit three simple bivariate linear regressions, in which the $\log_{10}$ count of abundant infestations was associated with (1) $\log_{10}$ count of hexagons, (2) $\log_{10}$ count of ecoregions and (3) residence time. We fit separate regressions because the tight correlation between counts of hexagons and ecoregions precluded a single interpretable model. To visualise relationships between the four variables, we plotted the correlation between habitat breadth and area of occupancy while visualising abundance and residence time via the size and colour of points. We fit an additional linear regression comparing residence time across species that met different dimensions of commonness. We assessed model fit and diagnostics and used the standardised residuals from each model of abundance to quantify each species' position relative to an expected abundance given habitat breadth, area of occupancy, and residence time. Species with higher-than-expected numbers of abundant infestations relative to their hexagon count, ecoregion count, or residence time could be more likely to have negative impacts on local ecosystems in areas where they are able to establish. In contrast, species with lower-than-expected numbers of abundant infestations could be cosmopolitan non-native species that are less likely to become abundant and locally problematic. Given the strong relationship between abundance and ecological impact (e.g., Bradley et al. 2019; Pearse et al. 2019), we focus on higher-than-expected abundance as a potential risk factor indicative of invasiveness.

2.4 | Geography of Underreported Non-Native Plants

To inform monitoring of non-native species for natural resource management, we calculated the species richness of all non-native species as well as the number of non-native species with abundant infestations within EPA Level III ecoregions (Omernik and Griffith 2014) spanning the conterminous United States. We appended states associated with each ecoregion to inform state-level watch lists of potentially invasive plants—we chose to create lists of species with abundant infestations based on ecoregions rather than states to overcome some spatial biases due to lack of data collection or reporting in some states. We visualised the current reported distribution of occurrence and abundance records within 50-km maximal diameter hexagons.

To better understand the geography of where non-native plants are likely underreported, we constructed sample-size based rarefaction/extrapolation curves (Chao and Jost 2012) for each ecoregion using the iNEXT package in R (Hsieh et al. 2016, 2020) with a datatype of abundance and all default settings. For each ecoregion, the count of observations of each species' occurrence was used to estimate total richness of non-native species, while the count of observations of abundant infestations was used to estimate total richness of non-native species with abundant infestations. Using the rarefaction/extrapolation curves, we predicted species richness at twice the observed sample size for each ecoregion, at which point the curves had saturated for all ecoregions. We calculated non-native species deficits as predicted minus observed species richness and fraction observed as observed divided by predicted species richness. We note that this is a non-standard prediction of species richness; this dataset fails several assumptions of optimal rarefaction/extrapolation (e.g., the data are not collected randomly, the dataset uses different collection methods, the system is not closed). Thus, the results can be used as a general guide to identify regions where higher levels of under-reporting of non-native species are likely (e.g., Laginhas et al. 2023). To support invasive plant policy and management at the state or local scale, we created a summary database with observed and estimated species richness of all non-native species and abundant non-native species.

3 | Results

We compiled 4,844,963 geolocations for 1874 non-native plant species observed in at least one location in the CONUS (Appendices S1 and S2, Figure S2). Of these, 797,759 geolocations for 1221 species reported high ($>10\%$) abundance of a non-native plant species. Of the 1874 non-native species in this dataset, 1101 (59%) showed one or more dimensions of commonness in the CONUS (Figure 1, Appendix S3). Eight hundred ninety two species (48%) occurred in at least 12 hexagons (widespread), 855 species (46%) occurred in at least 5 ecoregions (habitat generalist), and 805 species (43%) had at least 5 reports of high abundance (abundant). Canada thistle (*Cirsium arvense* (L.) Scop.), white clover (*Trifolium repens* L.), and common mullein (*Verbascum thapsus* L.) were the most widespread species, occupying 1858 (36%), 1850 (36%), and 1658 (32%) of the 5117 50-km hexagons, respectively. A similar set of species inhabited almost all of the Level 3 ecoregions, with yellow sweet clover (*Melilotus officinalis* (L.) Lam.), curly dock (*Rumex crispus* L.), *T. repens, and V. thapsus* found in all 84 ecoregions. Species with the most reports of abundant infestations were *C. arvense* ($n=57{,}813$ reports), common reed (*Arundo donax* L.; $n=36{,}468$), spotted knapweed (*Centaurea stoebe* L.; $n=36{,}085$), and leafy spurge (*Euphorbia esula* L.; $n=32{,}911$). A total of 565 species (30%) were common in all three dimensions: widespread, habitat generalists, and locally abundant in the CONUS (Figure 1).

3.1 | Commonness Versus Invasiveness

With each additional dimension of commonness that a species met, it was more likely to be identified as invasive by the Global Plant Invaders database (Laginhas and Bradley 2022) and/or by RIIS (Simpson et al. 2022). Species that met a single category of commonness were more likely to be identified as invasive than uncommon species ($\beta=0.47\pm0.16$, $z=3.03$, $p=0.002$), as were species that met two ($\beta=1.33\pm0.15$, $z=8.78$, $p<0.0001$) or all three ($\beta=2.20\pm0.15$, $z=14.40$, $p<0.0001$) categories of commonness. Uncommon species were the least likely to be identified as invasive (Figure 2), although 366 of the 773 uncommon species (47%) were identified as invasive by RIIS and/or Global Plant Invaders. Conversely, 20% ($n=223$) of the 1101

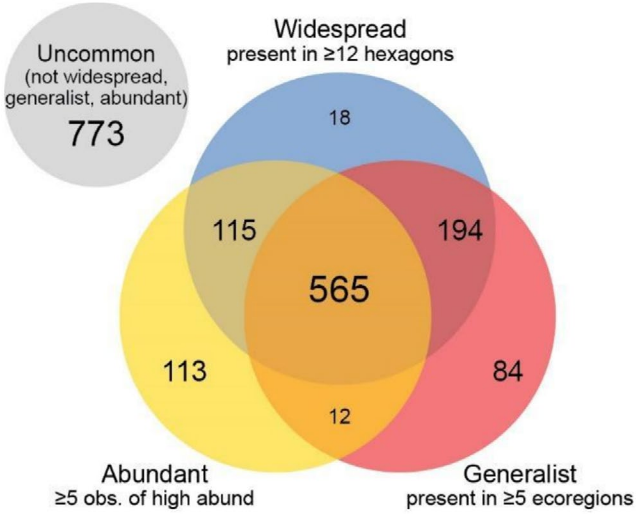

FIGURE 1 | Dimensions of commonness for 1874 non-native plant species in the CONUS. Of the 1101 non-native species that meet at least one criterion of commonness, the largest group of non-native species is widespread (892 total species). Note that areas are not proportional to the number of species, but larger numbers are presented in a larger font for emphasis.

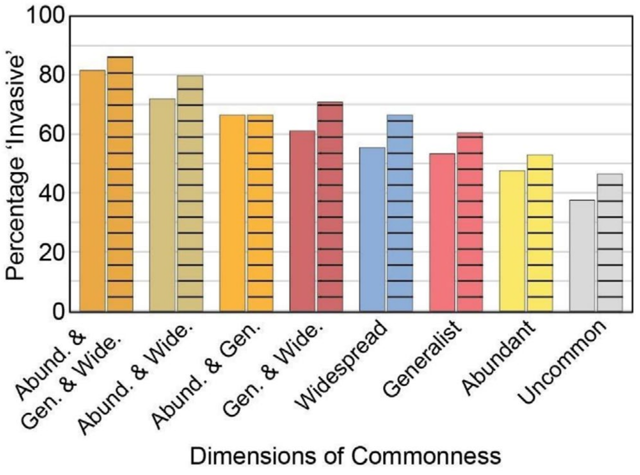

FIGURE 2 | Percentage of non-native species in each dimension of commonness that are also identified as invasive in the Global Plant Invaders (GPI) database (solid bars; Laginhas and Bradley 2022) or by the United States Register of Introduced and Invasive Species (RIIS) database (hashed bars; Simpson et al. 2022). Species achieving multiple dimensions of commonness are more likely to have been identified as invasive in other datasets. Colours follow Figure 1. Numbers of species in each category are shown in Figure 1.

common species (including 62 achieving all three dimensions of commonness) were not identified as invasive by either RIIS or Global Plant Invaders. Common species that were categorised as invasive had larger distributions and more reports of abundance (mean number of (n) hexagons: 153 ± 8.5 standard error (SE), mean n ecoregions: 19 ± 0.62 SE, mean n high abundance: 885 ± 125.8 SE) than common species that were not categorised as invasive (mean n hexagons: 32.4 ± 3.4 SE, mean n ecoregions: 8.5 ± 0.53 SE, mean n high abundance: 89.0 ± 33.5 SE).

3.2 | Correlations Between the Dimensions of Commonness

There was some degree of correlation between range size, habitat breadth, local abundance, and residence time (Appendix S1, Table S1). The relationship was very strong between the $\log_{10}$-transformed number of hexagons and the $\log_{10}$-transformed number of ecoregions in which a species occurs ($r = 0.94$; Figure 3), indicating that generalist species are also widespread. There was also a strong correlation between the $\log_{10}$-transformed number of hexagons in which a species occurs and the $\log_{10}$-transformed number of times an abundant infestation was reported ($r = 0.77$; Figure 4A), indicating that widespread species are reported as locally abundant in more places. The correlation between the $\log_{10}$-transformed number of ecoregions in which a species occurs and the $\log_{10}$-transformed number of times an abundant infestation was reported was moderate ($r = 0.63$; Figure 4B), indicating that generalist species are somewhat likely to be locally abundant.

In general, residence time varied considerably (Appendix S3), with documented establishment as recent as 2022 (*Halimodendron halodendron*) and as long ago as 1793 (*Prunus avium*). The correlation between residence time and the $\log_{10}$-transformed number of times an abundant infestation was reported was weak ($\rho = 0.15$; Figure 4C), indicating that species introduced a long time ago span the gradient from often to rarely being reported as locally abundant. Species that met multiple dimensions of commonness had significantly longer residence times compared to uncommon species ($\beta = 13.07 \pm 0.90$, $t = 14.46$, $p < 0.0001$, Figure S3).

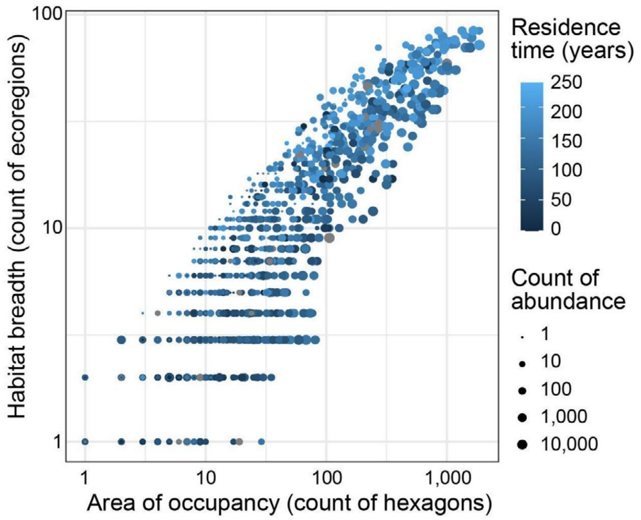

FIGURE 3 | Relationships between the dimensions of commonness, emphasising the tight correlation between area of occupancy and habitat breadth. Each point represents a species. Larger circles indicate a higher count of abundance and lighter blue indicates a longer residence time. Large, dark-coloured circles represent species that have many reported records of high abundance despite their recent introduction. Large circles in the lower left quadrant represent species that have many reported records of high abundance despite a small area of occupancy and narrow habitat breadth. Grey points represent species without an earliest record in Williams et al. (2024).

Species with higher-than-expected numbers of abundant infestations relative to the number of hexagons, the number of ecoregions, or residence time (points above the line in Figure 4) can be identified in Appendix S3 based on their standardised residuals. Redder colours indicate species that are particularly abundant relative to other factors of commonness, potentially indicating a higher risk of invasiveness. One hundred thirty two species had numbers of abundant infestations that were more than two standardised deviations above the regression lines for habitat breadth, area of occupancy, or residence time, with 41 species more than two standardised deviations above the regression lines for all three. Three species had standardised residuals of 3 or more for all three regression lines, indicating particularly high abundance. These species were Old World climbing fern (*Lygodium microphyllum* (Cav.) R.Br.), buffelgrass (*Pennisetum ciliare* L.), and paperbark tree (*Melaleuca quinquenervia* (Cav.) S.T. Blake). In contrast, 32 species had numbers of abundant infestations that were more than two standard deviations below the expected value based on the number of hexagons or the number of ecoregions; because many species had very low abundance despite long residence time, no species had residuals below two standard deviations relative to that regression relationship. The species with very few abundant populations relative to their habitat breadth, area of occupancy, and residence time include

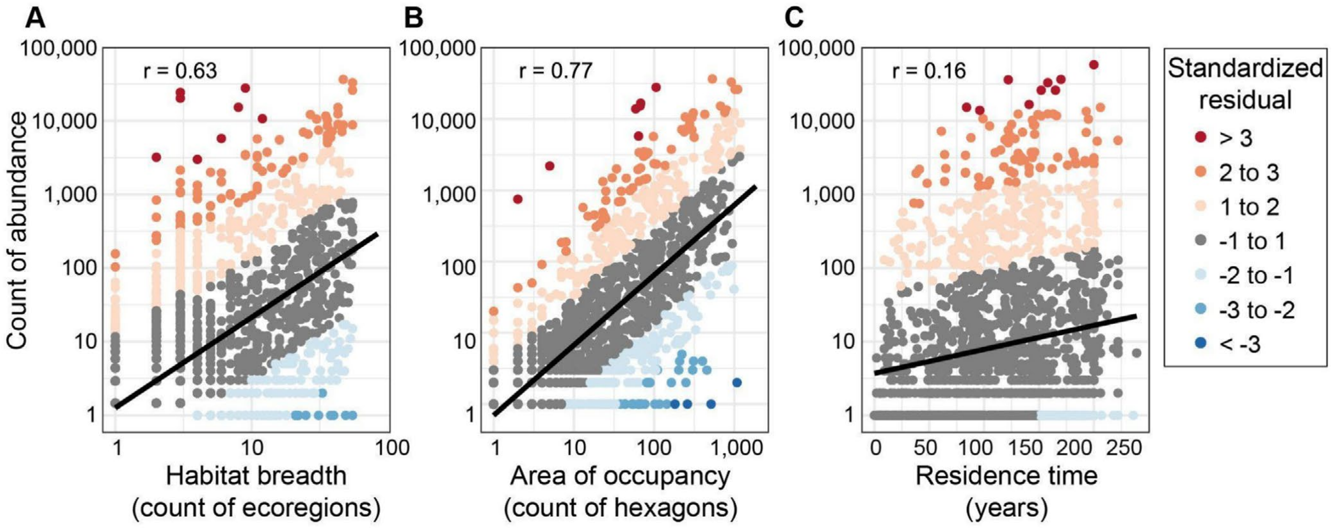

FIGURE 4 | Relationships between dimensions of commonness for the 1874 non-native plants in the CONUS used to identify species with higher-than-expected abundance based on their habitat breadth, area of occupancy, and residence time. (A) The correlation between the log10 count of ecoregions and the log10 count of abundant infestations is moderate (Pearson $r = 0.63$). (B) The correlation between the log10 count of hexagons and the log10 count of abundant infestations is strong (Pearson $r = 0.77$). (C) The correlation between residence time and the log10 count of abundant infestations is weak (Pearson $r = 0.16$). Black lines indicate the bivariate linear regression line, and each point represents a species, coloured by its standardised residual. Redder colours represent species with higher-than-expected abundance, which might indicate that a species is more likely to become abundant and impactful. Bluer colours represent species with lower-than-expected abundance, which might indicate that a species is less likely to become abundant and impactful. All axes except for residence time are presented on a log 10 scale.

several species commonly thought of as weedy in lawns or turf grass such as crimson clover (*Trifolium incarnatum* L.), henbit (*Lamium amplexicaule* L.), and chickweed (*Cerastium fontanum* Baumg.).

3.3 | Geography of Underreported Non-Native Plants

Richness of all and of abundant non-native species was highest in similar ecoregions, including most of California, forests surrounding the Great Lakes, the southeastern coastal plains, and the Northeast (Figure 5A,B, Appendix S3). Ecoregions of the intermountain west had a high reported richness of abundant non-native species, but only moderately high reported richness of all species. The ecoregion with the highest richness of non-native plants was 'California Coastal Sage, Chaparral, and Oak Woodlands', which contained a total of 744 non-native species and 478 species with one or more records of local abundance within the ecoregion. The mean non-native plant richness by ecoregion was 231 ± 12 (SE, median = 221) species. The mean abundant non-native plant richness by ecoregion was 63 ± 7 (SE, median = 71) species. The correlation between total and abundant non-native plant richness across ecoregions was strong ($r = 0.85$).

Based on predicted richness for all non-native species, the mean estimated deficit in observed non-native plants across ecoregions was 53 ± 3 (SE, median = 45). Ecoregions on the west coast, upper Midwest and Appalachians had the largest observation deficit, with the 'Coast Range' extending from Washington to California containing the largest estimated number of unreported non-native species (deficit = 150). Reports of non-native species in several ecoregions in the central United States are predicted to be missing 25%–37% of non-native species (Figure 5C–F, Appendix S4). The mean deficit in observed non-native plants with local abundance across ecoregions was 30 ± 2 (SE, median = 24). In contrast to richness deficits for all non-native species, Great Plains ecoregions in the central United States stand out as having higher observation deficits of abundant non-native species, with existing reports predicted to be missing 40%–69% of abundant non-native plants (Figure 5C–F, Appendix S4).

4 | Discussion

4.1 | Commonness Versus Invasiveness

Predicting which non-native species will become invasive is a primary goal of invasion science, and biogeographical characteristics of abundance and distribution are often related to invasive status (Catford et al. 2016; Fristoe et al. 2021). Species that have achieved large areas of occupancy and/or habitat breadth have demonstrated an ability to spread and species that have achieved local abundance are more likely to cause ecological harm (Sofaer et al. 2018; Bradley et al. 2019; Pearse et al. 2019). Although classical ecological theory suggests that most species are rare while few are common (Brown 1984; McGill et al. 2007), we identified an unexpectedly large number of common non-native plants: 59% met at least one dimension, with 30% of species meeting all three dimensions of commonness (Figure 1). Species that met at least one dimension of commonness included 223 non-native species that have not been identified as invasive either in the United States or in other regions of the world (Figure 2, Appendix S3). In contrast, many uncommon species ($n = 366$) were identified

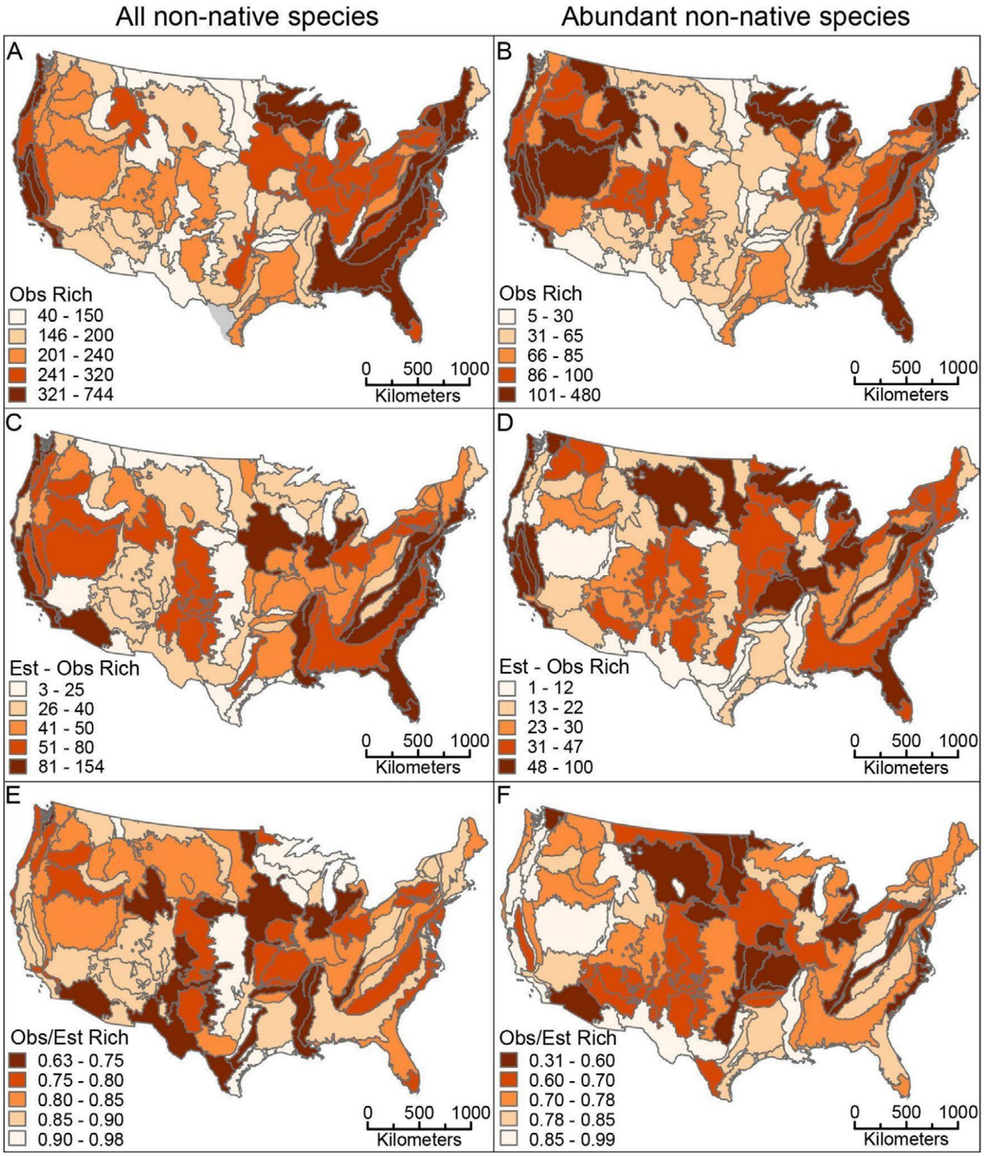

FIGURE 5 | Non-native species richness estimated across EPA Level 3 ecoregions of the CONUS. (A) Richness of all non-native species, (B) richness of abundant non-native species (species that have at least one abundant infestation within the ecoregion), (C) deficit of non-native species based on rarefaction and extrapolation curves, (D) deficit of abundant non-native species, (E) fraction of estimated non-native species that have been observed, (F) fraction of estimated abundant non-native species. Maps use an Albers equal area conic projection.

as invasive. This comparison of commonness to existing classifications of invasive species clearly demonstrates that invasive species are not consistently categorised based on abundance and distribution criteria and highlights the potential misclassifications of some non-native species (McGeoch et al. 2012).

Of greater concern for ecosystems is the misclassification of a non-native species as not invasive when it actually is invasive. Common species not classified as invasive were considerably less widespread than common species classified as invasive. It may be that some of these species are in earlier stages of invasion and have not yet been recognised as invasive by experts, possibly because they are common in states that do not monitor or report invasive plants. Common species not classified as invasive could be priorities for further risk assessment and potential management action. Conversely, many species identified as invasive are uncommon. Some of this discrepancy may be due to biases in spatial data collection (Pyšek et al. 2008) leading to a lack of information about the distribution and abundance of species that are actually common. It is also likely that experts in some regions have proactively listed species as invasive based on the need to follow a precautionary principle with biological invasions—an ideal scenario in invasive species management because it could support the containment or even eradication of some populations (Justo-Hanani and Dayan 2021). In some cases, it may also be possible that species were mistakenly labelled as invasive and would instead be better characterised as established non-native species. Although there is always a risk that uncommon species, particularly those that have recently arrived, will become invasive or have an outsized impact relative to their distributions, limited management resources are likely to be most effective if they focus on locally or regionally uncommon species that have already demonstrated that they can become abundant and widespread elsewhere.

4.2 | Correlations Between the Dimensions of Commonness

Understanding the relationships between species abundance and distribution is also a long-standing goal of biogeography (Brown 1984; Sporbert et al. 2020). Abundance and range size are expected to be correlated (Gaston 2003). For non-native plants in the CONUS, this analysis reveals a strong correlation between area of occupancy and local abundance, a moderate correlation between habitat breadth and local abundance, and a weak correlation between residence time and local abundance (Appendix S1, Table S1). We also see a very strong correlation between area of occupancy and habitat breadth. These relationships were much stronger than correlations found in a comparable analysis of non-native plants in Europe (Fristoe et al. 2021), indicating that geographical relationships between abundance and distribution may be inconsistent across different geographies. Taken together, these findings highlight the importance of interactions between non-native plants and recipient ecosystems, with widespread species often but not always achieving the level of local abundance likely to lead to ecological impacts (Sofaer et al. 2018; Bradley et al. 2019; Pearse et al. 2019).

Because abundance is strongly correlated with ecological impact (Bradley et al. 2019), species that are more frequently abundant than expected given their distribution or residence time (redder points in Figure 4) are prime candidates for further risk assessment to determine their invasion status in the United States (Sofaer et al. 2018; Bradley et al. 2019; Pearse et al. 2019). By using Appendix S3 to identify species with higher-than-expected abundance (visualised with red in Figure 4), practitioners can create watch lists of potentially invasive species. For example, the biennial shrub 'Pride of Madeira' (*Echium candicans* L.f., 1782) is locally abundant in over 200 localities in California, abundance values that are more than one standard deviation higher than expected relative to their habitat breadth, ecoregions, or residence time. Similarly, the perennial shrub waxyleaf privet (*Ligustrum quihoui* Carrière) is locally abundant in over 900 localities in Texas and has abundance values two standard deviations above expected. Neither species has been recognised as invasive on state, national or international lists (Laginhas and Bradley 2022; Simpson et al. 2022). Many locally abundant plant species are readily available as ornamentals and may therefore be able to quickly expand outside of their current geographies (Beaury et al. 2021), thus, state invasive species councils could prioritise species with higher-than-expected abundance (Appendix S3) for risk assessment and potential regulation.

4.3 | Geography of Underreported Non-Native Plants

Geographies of potential abundance (Figure 5, Appendix S4) could further refine state watchlists of potentially invasive species. For example, Brazilian peppertree (*Schinus terebinthifolia* G. Raddi) has higher-than-expected abundance and is recognised and regulated as a noxious weed in Florida and Texas. However, our analysis at the ecoregion scale illustrates that the species invades the Southern Coastal Plain and Western Gulf Coastal Plain ecoregions (Appendix S4), which extend across the Southeast, from Texas to South Carolina. Thus, recognising and regulating the species across the Southeast could make for a more proactive regulatory landscape and prevent future introductions and invasions in states outside of Florida and Texas (Beaury, Allen, et al. 2023).

An ecoregion-based approach for identifying potentially problematic non-native plants can help to overcome some of the spatial biases in data collection. In the above example of *S. terebinthifolia*, the species has not been reported outside of Florida and Texas. However, the lack of occurrences in neighbouring states could be due to the lack of data collection in southeastern states, which cause large deficits in the reporting of abundant non-native species (Figure 5C,D), rather than low risk of invasion. Similarly, only three non-native species have been reported as abundant in the state of Delaware in the assembled database (*Celastrus orbiculatus* Thunb., *Lonicera japonica* Thunb., *Microstegium vimineum* (Trin.) *A. Camus*) but 91 non-native species that are abundant in the United States are also abundant in one or more of the ecoregions that overlap the state of Delaware (Northern Piedmont, Mid-Atlantic Coastal Plain and Southern Plains; Appendix S4). Thus, invasive species councils could use the lists of non-native species that already occur or are abundant within ecoregions associated with their state (Appendix S4) to guide state risk assessments to focus on the species most likely to affect local ecosystems.

While an ecoregion-based approach can support more consistent identification of invasive plants in some states, some regions clearly suffer from a large-scale information deficit. For example, little information on abundant infestations has been reported across Great Plains states (Appendix S1, Figure S2), leading to a high observation deficit (Figure 4). These large observation deficits could mean that abundant infestations go unnoticed and untreated, leading to more costly and less effective management later if species spread (e.g., Rejmánek and Pitcairn 2002; Keller et al. 2007). Further, rarefaction and extrapolation curves optimally use data from closed communities (no new species being introduced) that have been comparably sampled. New species are likely arriving to United States ecoregions and there are strong spatial biases in data collection (Appendix S1, Figure S2). In both cases, failing to meet the assumptions of rarefaction will generally lead to an undercount of non-native species and an underestimate of deficits in non-native species richness. Although all regions are likely undercounting non-native species, states with larger observation deficits could consider investing more effort in collecting and reporting occurrence and abundance information to open-access repositories like EDDMapS (Bargeron and Moorhead 2007). Standard categories used to collect abundance information across the United States have been compiled in Bradley et al. (2018) and could be used to guide future mapping and monitoring efforts.

4.4 | Conclusions

Even with spatial biases in data collection, there are hundreds of common, non-native plants in the CONUS. Although there is little information on the ecological impacts for most of these common species, distributional ranges play an important role in risk assessment by identifying where species can potentially establish (e.g., Roy et al. 2018). The ecoregions and habitats where non-native plants become abundant (Appendix S4) can inform the risk assessment criterion of whether species have the potential to spread into natural areas (e.g., Buerger et al. 2016; Bradley et al. 2022). Lastly, the quantity of observations of local abundance within a given ecoregion can serve as a proxy for ecological impact given the negative relationships between non-native abundance and native species abundance or diversity (Sofaer et al. 2018; Bradley et al. 2019; Pearse et al. 2019). Thus, the geographic information presented here addresses many of the criteria needed by states to evaluate the invasion status of the species.

Although there are many scattered sources of spatial information for invasive plants (Crall et al. 2006; Fusco et al. 2023), they remain challenging to compile and harmonise. Substantial previous work has focused on non-native plant distribution and richness (van Kleunen et al. 2019), but these may be poor proxies of abundance and impact (Seabloom et al. 2013). Here, by aggregating and standardising all available spatial information about non-native plant abundance, we provide a comprehensive view of the non-native plant flora in the CONUS (Appendix S2). This database can inform further biogeographical analyses of relationships between species abundance and distribution. This information can further inform risk assessments within federal, state, and local jurisdictions using the precautionary principle to proactively identify and prioritise common and potentially invasive species. Geographical information can also help to identify priority candidates for early detection and rapid response to invasion, leading to more consistent and proactive invasive species management across the country.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Appendices S2–S5 are available at https://doi.org/10.7275/ir-55258. R code used to create Figure 4 (correlation plots) based on Appendix S3 and R code used to calculate species area curves and associated estimates of non-native species presence and abundance in Appendix S5 are both archived at https://doi.org/10.7275/y1f1-9m81.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.